ON THE MODE OF DISSEMINATION AND ON THE RETICULATIONS OF *RAMALINA RETICULATA*.

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SEVERAL years ago, Professor W. G. Farlow, of Harvard University, suggested my examining the thallus of *Ramalina reticulata* Krplhbr., with a view to determining the origin and mode of growth of the holes which give to this plant its characteristic appearance and its name. He generously allowed me to use all the material which was in the herbarium, but for various reasons I failed to obtain any results.

On coming here, I was surprised to find the white and blue oaks (*Quercus alba* L. and *Q. Douglasii* Hook. & Arn.) festooned with this lichen to such a degree that many even young and small trees are as hoary in appearance as old New England pines overgrown by *Usnea barbata* Fr.[1] The live oaks (*Q. chrysolepis* Liebm.) of this vicinity are seldom the resting place of other than fragments of nets torn by storm and wind from other trees and blown to them. As a rule, the evergreens, whatever the shape of their leaves, have fewer fragments or whole plants of Ramalina growing upon them than deciduous-leaved plants. It would be a long and useless task to determine the species of shrubs and small trees which, forming the thickets on the borders of the creeks, and composing the "chapparal" covering parts of the foothills, are draped more or less by large or small fragments of Ramalina which have been caught in winter by their leafless branches, or on which the younger nets have grown from the spore. The reasons why *Ramalina reticulata* is found hereabouts on deciduous-leaved trees and shrubs almost exclusively are obvious: namely, that there is less chance of fragments catching

[1] The accompanying figure shows a white oak overgrown by *Ramalina reticulata*. The photograph of which this is a reproduction was very generously taken for me by one of my students.

on branches covered by leaves than on bare and rough ones; and if any fragments should catch on leafy branches, they would receive less light during the winter rains than those hanging from unshaded branches, and hence, as the elaboration of non-

nitrogenous food by the gonidia would be less, so also the growth of the association of hyphæ and gonidia would be proportionally less. However, nearer the coast and southward, there is not this distinction, for this lichen grows on trees and shrubs of all sorts in that milder region, where during the dry and leafy season frequent fogs make some food manufacture and growth even then possible. About here it grows with little competition and attains a startling size, but there it is crowded by Usnea, Cladonia, etc., and remains, so far as my own observations go, much smaller in size. I have a fragment, collected very near here, which is twenty-six inches long, measured dry. There is no means even of guessing how much longer the whole plant would have been. So far as I know, this species of Ramalina is the longest lichen however, and as the breadth of the fragments is never very small in proportion to their length it may come near being the broadest also.

MODE OF DISSEMINATION.

By all means the commonest and most effective means by which *Ramalina reticulata* is reproduced and distributed is by larger or smaller pieces being torn by the wind from plants firmly attached, and carried to trees or shrubs, on the bare, rough branches of which the fragments catch and stay (fig. p. 405). As will be shown later on, this lichen softens to a remarkable degree when wet, it absorbs much water and greatly increases in weight, and its netted structure and branching habit cause it to be easily torn as it hangs down like a soft, delicate piece of gray-green lace, always longer than it is broad. When dry, it is hard, stiff, tenacious, and elastic, not readily broken by the wind. When wet, it is soft, pliant, not especially tenacious or elastic, and it is *much* heavier. As a rough index of the increase in weight during a hard and protracted rain the following figures will serve.

Fragment air dry weighed	- - -	0.499 gr.
" soaked 15 min. in cold[2] water and surface dried by filter paper, weighed	- -	1.020 gr.

Weight wet: weight dry = 2.04 : 1.

This increase in weight is less than that which would occur in nature, for more water would there adhere to the surface of the lichen than was left by the filter-paper. The increase in weight is furthermore unaccompanied by any immediate increase in strength,[3] for it is impossible that growth should occur so promptly or so rapidly as to keep pace with the increase in weight, although the wetting and consequent increase in weight take place more slowly in nature, even in a hard rain, than when the lichen is immersed in water in the laboratory.

The rains come only in winter, when the branches of many trees and shrubs are bare of leaves, and roughened by buds and barky excrescences. The rains are usually accompanied by wind, often high wind. It is therefore easy to see that the tearing away by the wind of fragments from the soft, heavy, pendant

[2]Cold water to avoid possible solution of gelatinous matter.

[3]For the actual decrease in strength see p. 415.

masses of lichen is inevitable, that the catching of these, often with a double twist which fastens them securely on bare rough branches, is very likely to occur ; and when the rain ceases, and

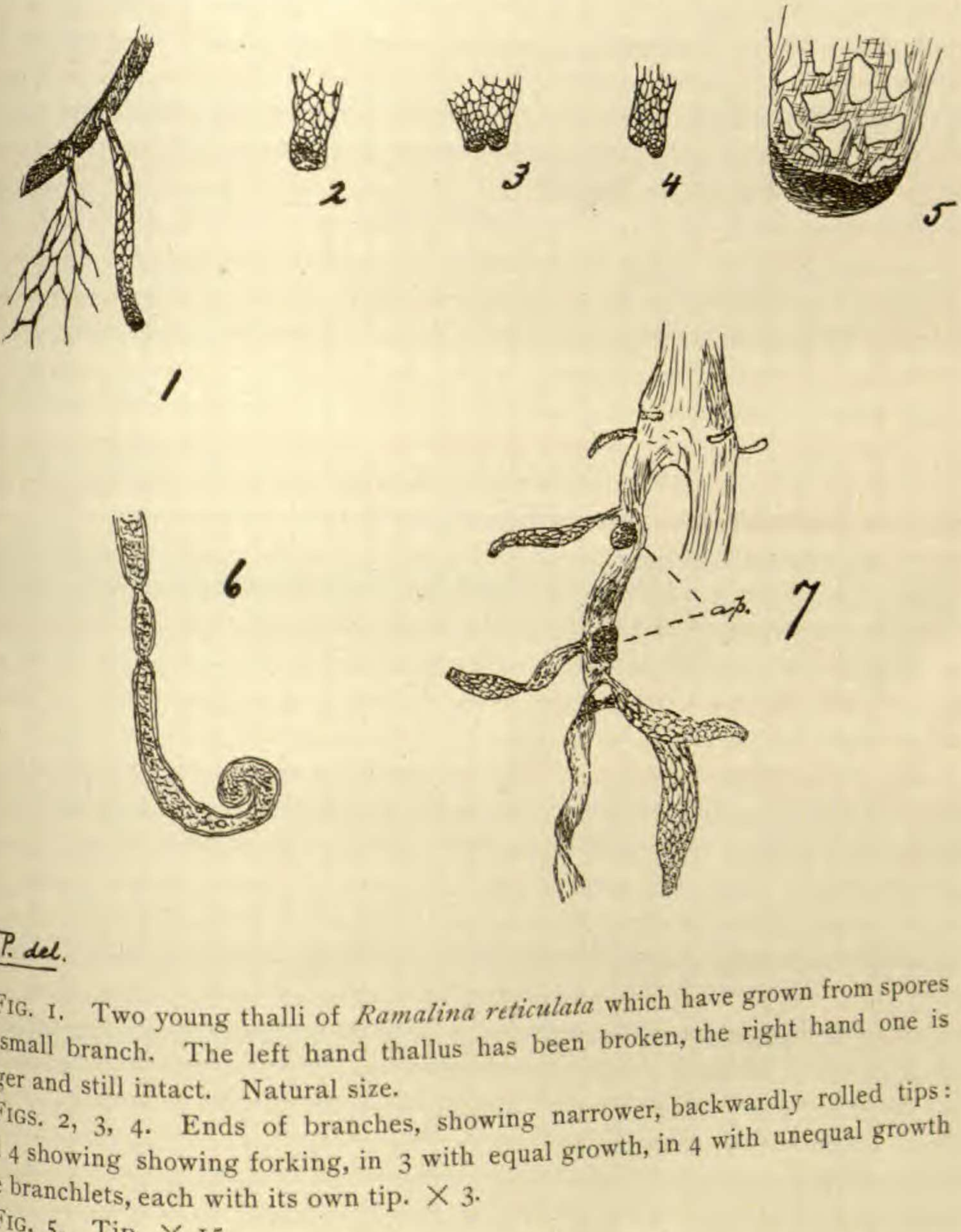

FIG. 1. Two young thalli of *Ramalina reticulata* which have grown from spores on a small branch. The left hand thallus has been broken, the right hand one is younger and still intact. Natural size.

FIGS. 2, 3, 4. Ends of branches, showing narrower, backwardly rolled tips: 3 and 4 showing showing forking, in 3 with equal growth, in 4 with unequal growth of the branchlets, each with its own tip. × 3.

FIG. 5. Tip. × 15.

FIG. 6. Tip in section, showing circinate rolling. × 96.

FIG. 7. Part of a large thallus, showing apothecia (*ap*), and branches of various sizes, on the broad strands bounding a large mesh. Natural size.

the lichen dries, it contracts somewhat where it has been caught, as well as along its whole length and breadth, and so holds still more tightly to its support. It thus remains firmly fixed till the next rain comes. It may be dislodged again, for such fragments do not form even the small weak holdfasts developing on specimens which have grown from the spore (fig. p. 407). The dislodgement is, however, less common than one would at first imagine ; *first*, because of the "double turn" which is so common, and *second*, because the part thrown around the branch remains more or less fixed in shape, conforming to the branch somewhat as a tendril does to its support. That there is anything more than a mechanical reason for this I doubt, although there may be contact or chemical irritation at this point ; for even when thoroughly wet, the part of the lichen bent or coiled around a branch does not uncoil or become very loose. Whether this is simply the fixing of a certain form by the growth, completed under mechanical stress, of the part of the lichen bent around the branch, or whether the growth is modified, directed, prolonged and finally terminated by the irritation set up by contact with the branch, I am not now able to say. Experiment only can settle this point, and experimentation with lichens is peculiarly difficult because of their slow growth. Against the idea that there may be irritation (contact or chemical), and a response thereto on the part of the hyphæ, is the fact that these hyphæ do not grow out from the lichen and attach themselves to the bark, there is no formation of anything like a new foot or holdfast such as the young lichen forms when growing from the spore. It is necessary, however, to consider the effect of contact with a branch not only upon the hyphæ which touch it, but also upon the the gonidia and hyphæ which may receive more or less nutritious solutions from the dead and decaying bark-cells. Observation leads to the belief that the fragment is simply caught by a rough branch, twisted about this by the wind, and remains there indefinitely, or until, during some subsequent rain, it becomes detached, falls to the ground, or is blown away to another branch.

The growth of any part of the lichen seems not to be impaired by detaching it from any other part. The fragments torn and carried away by the wind grow and fruit perfectly well ;

indeed it is a difficult matter (if possible at all) to find a whole fruiting specimen of *Ramalina reticulata.* I have not done so. The only specimens showing the holdfasts which I have been able to find, are small, the largest only seven inches long, (measured dry). Judging by the size of these holdfasts, it is hard to believe that they would grow strong enough to hold plants much longer; and of course the rest of the thallus is as weak as the holdfast, and that it breaks readily has just been shown.

Plainly then the usual and most effective mode of reproduction and distribution of *Ramalina reticulata* is a vegetative one, the rain softening the thallus and making it possible for the wind to detach pieces, even of considerable size, which are then carried (a large proportion of those detached) and fastened more or less securely by the wind upon branches of trees and shrubs, where the fragments thrive as if always undisturbed.

THE RETICULATED THALLUS.

The characteristic feature in the habit of *Ramalina reticulata* is, as the name implies, its netted structure. From the youngest and smallest to the oldest and largest, these Ramalinas are all of them nets. The youngest (and the young branches reproduce this) are shaped something like a narrow spatula (*figs. 1, 2*). Just behind the backwardly rolled and somewhat narrower tip, the flat thallus begins to be perforate, these perforations increasing in size to near the base of the thallus. There they are decidedly smaller, finally disappear, and the thallus contracts into a single thickened strand, which enlarges at the base. The stalk of a branch is very short and is confluent with the thallus (*fig. 7*, also *figs. 3* and *4* where branching is taking place). In the young Ramalinas which have grown from the spore, on the branches of trees, etc., the stalk may be somewhat longer and slightly broadened at the base into a small flattened, discoid holdfast (*fig. 1*). Since neither the stalk nor the holdfast keeps pace with the growth of the net-like part of the thallus, it is easy to see that the increasing weight of the last will sooner or later result in the lichen being broken or torn into two pieces.

This lichen does not form soredia. Other than the strictly vegetative mode of reproduction, which has been described in the foregoing, the only mode is by spores. The apothecia in which these are produced form on all older, though not necessarily oldest, parts. Either a very few comparatively large ones are produced on the flat, narrow strands forming the coarser nets, or a few still larger ones are scattered over the broad, usually short, plates, from which many branches spring, or finally a great number of small ones arise on similar, but older, broad expanses. The apothecia usually form on the flat surface rather than on the edge of the thallus, thus exhibiting a tendency directly opposite to that of the branches; but there are exceptions to both parts of this rule (*fig. 7 ap.*).

The origin of the holes in the thallus of this lichen has been discussed in several papers already. Of these I have been able to see only three, namely, Agardh's original papers,[4] in which he first describes the plant as an alga, and Lutz's.[5] In the last, various papers are cited. After summarizing and criticising the views of his predecessors, Lutz proceeds to describe his own experiments and conclusions. He worked only with dried herbarium material, and had never seen the plants in nature. His observations were, therefore, necessarily limited, and his results are naturally incomplete. Indeed, the obscurity and uncertainty regarding this lichen are due to the unnatural conditions under which small quantities of it have been examined, from the time when Agardh acquired some of it, supposed it to be an alga, and named it "*Chlorodictyon foliosum* (J. Ag. mscr.) Hab. . . . in Hb. J. E. Gray. (sine ulla de origine et loco adnotatione),"[6] until now.

Lutz calls attention to the gelatinous material in which the outer hyphæ are imbedded, and to the fact that, because of this, the outer parts at least will swell when moistened. He cut ter-

[4] (*a*) *Chlorodictyon.* Öfvers. af K. Vetensk. Akad. Förhandl. no. 5, 1870; and, (*b*) Lund's Univ. Arskr. 9: 23. 1873.

[5] Ueber die sogenannte Netzbildung bei *Ramalina reticulata* Krplhbr. Ber. d. Deutsch. Bot. Gesellsch. 12: 7. 1894.

[6] *Ibid. a.* p. 434.

minal portions from dry herbarium material, and measured the expansion which took place when water was brought into contact with them. He found that the expansion was from 20 to 43 per cent., and the more rapid the thinner the pieces. All parts, old as well as young, expand on wetting; all parts expand unequally if the water is unequally distributed over them; and if water is applied to only one side or edge of the thallus, or thallus fragment, that side will expand first and most, the transfer of water from part to part being comparatively slow. Such unequal expansions also occur in nature, because raindrops fall first on some parts, then on others, though during a rain-storm of longer duration all parts become uniformly moistened. The unequal wetting and consequent unequal expansions develop strains which tend to pull apart the thallus, the moist, soft parts pulling against and away from the dry, stiff parts in all directions. The majority of the hyphæ run longitudinally, the outer ones more regularly than those within; and the thallus is thin.

The result of wetting is that the thallus increases somewhat in thickness, more in length, and most (proportionally) in breadth. For example, a thallus branch, which I measured, was

$1\frac{13}{32}$ inches long $\frac{9}{32}$ inch broad	when air dry, - - - - - -	35.7mm 7.1mm
$1\frac{22}{32}$ inches long $\frac{13}{32}$ inch broad	when soaked for 3 minutes in cold water, -	42.8mm 10.3mm

$\frac{9}{32}$ inch=increase in length=7.1mm=20 per cent.
$\frac{4}{32}$ inch=increase in breath=3.2mm=44 per cent.[7]

The most evident reason for this greater proportional expansion in the breadth is that the gelatinous material, on absorbing water, is met by less resistance to swelling outward (transversely) against the air, than longitudinally against other gelatinous matter and the hyphæ towards the tip and the base from the wetted part.

From the unequal expansions, the proportions of which I have roughly measured and indicated in the above table, Lutz

[7] The metric figures in this table are *calculated* from the figures in inches, which were obtained by *measurement*.

concludes that the perforations may readily arise by simple pulling apart of the generally longitudinally running hyphæ, adding that the breaks appear in the weakest parts of the thallus, namely in the thinnest parts, where the "bark" layer is virtually absent and where the spherical gonidia are most abundant (they are nowhere uniformly distributed), for in such places the hyphæ cannot bind them tightly together. This is true, but it is not all the truth. Microscopical examination of living material shows that the hyphæ are not merely in contact with the gonidial cells but are attached to them by haustoria which penetrate the cells,[8] and that the hyphæ bind the gonidia together in fairly coherent masses *except* when the gonidia have divided so rapidly that the young cells are not yet held fast by haustoria, though the mass and even individual cells may be enmeshed by hyphæ. The region of most frequent and most rapid multiplication of gonidia is that near, though not necessarily next to, the tip, and even in fairly old parts, such divisions of gonidial cells occur, and necessarily occur, if in these parts the hyphæ are to be adequately supplied with food-furnishing cells. To some degree in all parts of the lichen thallus, therefore, and most in the younger parts near the tips, there will be masses of young and small gonidial cells not yet held firmly by investing and penetrating hyphæ, and these masses will form the less coherent parts of the thallus, which can be more readily torn through by the unequal and mainly transverse expansions produced by unequal wettings.

But Lutz, though he mentions the peculiar tips of the branches of the thallus of *Ramalina reticulata*, overlooks the part they play in the formation of holes. The tips (*figs. 2, 3, 4, 5*) are narrower than the thallus just behind, and are rolled over. A section of the tip is crozier shaped (*fig. 6*). If a short branch, a few millimeters long, is put convex side down (that is, with the apex pointing upward) on a horizontally placed slide, and a drop of water put on the upper surface of the branch near the apex, the apex will be pushed forward by the longitudinal

[8] I shall discuss this in detail in a subsequent paper.

expansion of the thallus, but the youngest part will expand more, the apex itself will swell like the rest of the thallus in all three directions (in length, breadth, and thickness) and will bend upward slightly and then curve backwards somewhat over the thallus, thus straining the flat young part of the thallus just behind. But if the experiment be modified by placing a similar branch convex side down on a drop of water already on the slide, the apex will curl much more and much more rapidly, and thus the strain on the young parts just behind will be much greater. Because the apex is always narrower than the flat part of the thallus, and because it is always circinately curved, it cannot expand so much as the part behind. The young flat part is furthermore less coherent than either the closely rolled apex or the older flat parts farther back, because of the rapid multiplication of the gonidial cells and the consequently feeble attachment (if any) of the hyphæ to them. The apex then, in folding over, pulls the young flat part on the convex side, thus straining it longitudinally and inducing transverse ruptures in it. At the same time, the thallus is expanding transversely in the same part, but expanding most at a point not immediately behind the apex, for the narrower circinate, and, therefore, thicker apex opposes transverse expansion in the flat thin part closest to it. Precisely where the longitudinal strain is greatest, inducing transverse ruptures in the looser gonidial areas, there the transverse strain is also greatest, inducing longitudinal splits in the same gonidial areas.

Thus we see that it is not simply the expansion, or the unequal expansion, in three directions which produces the holes in the thallus of *Ramalina reticulata*, although this is the main factor in the older parts (where the formation of new holes is less frequent), but it is also the curving and consequent straining longitudinally of the softest and least coherent parts of the thallus, near the tip, by the folding over of the apex, and the concentration, owing to the narrowness and circinate curvature of the apex, of the greatest transverse strain in that zone where the longitudinal strain is also greatest.

Such experiments as those just described can be performed on intact thalli or larger fragments, either in the laboratory or in nature, quite as well as upon small pieces on the stage of the microscope. The dry thallus may not be able to retain the whole of a drop of water, but some of it will be held by the gelatinous outer part; there expansion will take place, and, if enough water has been held, curvature also. The nearer the tip the point is upon which the drop falls, the thinner it will be, the more prompt and the greater will be the expansion, the more pronounced the curvature, the greater the strain, the less coherent the structure of the thallus, the greater the likelihood of ruptures occurring in the weakest areas. Except when rain falls unaccompanied by any wind, and except in fog, the thallus is not likely to be uniformly wetted and in the former case uniform wetting would not be accomplished immediately. So in nature the conditions of expansion and curvature, as demonstrated by experiment, are normally realized.

Lutz says that drying after wetting brings about a change in the shape of the thallus, the length being greater, the breadth less, but the area the same as before the water was supplied; and that these contractions and changes in shape produce new and enlarge already existing holes. If such changes normally took place on drying, holes would result; but they do not take place. Lutz's method of experimentation is probably to blame for his conclusion. He used such small pieces of lichen that his experiments were conducted on the slide, under a magnification of thirty diameters. The moistened gelatinous matter on the surface of the lichen would naturally adhere to the glass somewhat, enough at least to prevent perfect contraction to the original form, and, as his fragments were several times longer than broad, there would be most adherence and least contraction longitudinally, which was what he found. I allowed the fragment which I had used for determining the expansion on wetting, in the experiment above reported, to dry quite free of such adherences by hanging it up. It contracted within five hours to

$1\frac{13}{32}$ inches in length $= 35.7^{mm}$
and $\frac{10}{32}$ of an inch in breadth $= 7.9^{mm}$.

that is, to the same length exactly and to within $\frac{1}{32}$ of an inch of the original breadth.

Two more points should be noted in connection with the the formation and enlargement of holes; namely, the relative tensile strength of the lichen when dry and when wet, and the part played by growth. I have made tests of which the following may be taken as the average. A piece of thallus with large holes bounded by stout filaments and bands was hung, tip downward, from a hook of small iron wire (not so fine as to cut the lichen quickly. This hook passed through a hole in the mesh and the part above appeared to be of average strength. From a similar hook similarly placed below were suspended weights. The breaking strength of the two strands which held the hooks was 150 grams when dry. The lichen was then soaked for fifteen minutes in cold water and hung up again, after the surface water had been removed. I tried to select for the support of the wire hooks two strands of size and position as nearly as possible the same as before. The strands broke with a weight of 30 grams, 20 per cent. only of the weight carried when dry. The experiment is rude and has evident faults (for instance, the strands are not of uniform strength under like conditions, hence in testing dry the strongest strands may be used, thus leaving absolutely, as well as relatively, weaker ones for testing wet; and the whole thallus had probably been weakened by weighting dry, hence it was weaker when wet than it ordinarily would have been); but it has some value in indicating the quality if not the quantity of difference in tensile strength under the two conditions.

This experiment indicates the longitudinal tensile strength. The transverse tensile strength must be less. Microscopic examination of sections, and unsectioned but cleared fragments of the thallus, shows, as before stated, that the hyphæ run mainly longitudinally in strands, fewer obliquely, almost none exactly transversely. Evidently the transverse tensile strength, both dry and wet, would be less than the longitudinal. But I have shown that the length of a piece of thallus increases about 20 per cent. on wetting, whereas the breadth increases at least twice as much. From these figures we must infer that the transverse tensile strength must be much less when the thallus is wet than when it is dry. What the proportions are is not important.

These experiments and considerations show that, when the lichen thallus is being most strained by expanding and bending, it is also becoming weakest, namely when it is wet.

Growth, whether equal or unequal in different parts, would tend to enlarge those holes already formed. The growth of the longitudinally-running hyphæ, which form the strands bounding or between the holes, would lengthen these strands and cause them to bound larger holes. Unequal growth in young parts where holes had been formed either not all or only in small numbers, would produce strains favoring, if not wholly causing, the formation of holes at the points of greatest weakness. Growth takes place only when and where the lichen is wet and therefore mechanically weak. Growth would be unequal if the distribution of water in the thallus were unequal. That growth is unequal is evident from the fact that only very limited parts of the thallus are flat. The water-supply of different parts of the lichen will frequently be unequal, growth will therefore necessarily be unequal, growth strains will be unequal, the thallus will be most strained in weakest parts, these weakest parts will therefore be made still weaker. The growth of the new gonidial cells formed by the division of old ones will weaken and strain the part of the thallus where they are. If the growth of hyphæ and gonidia does not accomplish the formation of holes in the weakest parts, it at least facilitates it, and the strains produced afterwards by wetting, expanding, and curving, will do so. But growth is notoriously slow in lichens, and hence it cannot be an important factor in the formation of the holes as compared with the purely mechanical effects of wetting.

This explanation of the mechanics of hole formation presupposes the peculiar structure and composition of the thallus as a whole and the peculiar structure and mode of growth of the apex. Why the apex is consistently narrower and circinately inrolled, why the gonidia are distributed as they are, these are questions not answered by this mechanical explanation. They remain for further physical and physiological examination.

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